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Landscape Chorology of Springtails in the Taimyr Peninsula: 2. Latitudinal Species Differentiation

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Abstract—Zonal-landscape distribution of springtails along the latitudinal transect from northern taiga forests to polar deserts of the mid-Siberian sector of the Arctic Region was analyzed. Hyperarctic, euarctic, hemiarctic, and hypoarctic groups of species corresponding to the detailed subdivisions of the category "Arctic species" were distinguished on the basis of relative abundance indices. In the springtail fauna of Taimyr, the fraction of all these species, mainly associated with forestless subarctic landscapes, is rather large (more than 45% of the regional fauna), which is unusual for such a primitive group. The character of latitudinal distribution of springtails in Taimyr is rather similar to that typical of other taxa of terrestrial animals, and all the characters of the zonal-landscape distribution of species described in the literature can be exemplified by springtails.

The present communication treats on the typology of the latitudinal distribution of springtails of Taimyr, in other words, its goal is to reveal among them the real Arctic species, which are associated with northern forestless landscapes to the greatest extent, and also groups similar in the character of their association with particular parts of the tundra zone. No generally accepted criteria that could be used to unambiguously attribute a species as the Arctic, boreal, or nemoral, have been developed as yet, and two fundamentally different empiric approaches (and frequently their combination) are used in practice (Chernov and Matveeva, 2002).

The first approach takes into account only geographical borders of the species distribution, with quantitative indices of distribution disregarded. This purely biogeographical approach ignores the ecological features of the species distribution and is, apparently, inefficient for chorological purposes. Many typical Arctic arthropods are only "more characteristic" of Arctic territories, but are not limited in their distribution to within the Arctic borders (Kuznetsov, 1938; Chernov, 1978, 1984; Danks, 1981; Chernov *et al.*, 2001; etc.). Soil microarthropods are no exception to this general rule. For example, nearly all higher-latitude species of oribatid and prostigmatic mites populate not only Arctic Region, but also boreal landscapes (Makarova, 2002), and the majority of springtail species, traditionally attributed as Arctic species, move beyond the limits of high-latitude landscapes and penetrate far southwards via highlands and various intrazonal elements of landscapes. From the chorological point of view, these are meta-Arctic, Arctic-mountain, or Arctic-boreal, but not strictly the Arctic species.

The second approach considers to be the most important the character of the species distribution within its range, and the association of a species with a particular biome is assessed using quantitative indices of its abundance, frequency of occurrence, adherence, activity, and its association with various biotopes, i.e., is based on distinguishing the "zone of optimum" within the species range (Chernov and Matveeva, 2002). This approach is better substantiated ecologically, but is rather subjective because of the evident difficulties in the choice of the criteria.

One of the possible criteria of such an ecological approach is used in the present study, whose main goal was to reveal the "optimums" in the ranges of springtails of Taimyr on the basis of indices of relative abundance and latitudinal-landscape typology of the distribution of species of this taxon in the tundra zone.

MATERIALS AND METHODS

The material analyzed in the present study was described in detail in the 1st communication (Babenko, 2003). The method for calculation of "coefficients of relative association" (Pesenko, 1982) is also given there. It is only necessary to discuss some characteristic features in using this index for revealing the area of higher relative abundance of a species, which is identified as the "optimum" of the range.

The same original goal in collecting the material (to reveal to the maximum possible extent the specific fauna of a region and to describe the population structure of the most typical landscapes) resulted in that the same methods were used and samples were collected in all the main elements of the landscape series in each region of investigations. As a result, it was possible to use the previously collected material for the purposes of the present study on the following assumptions: (1) fluctuations in the abundance of springtails, observed in different years, are insignificant in comparison with its changes along the latitudinal gradient, which makes it possible to use data obtained in different years; (2) the plant associations examined do reflect the landscape diversity of a particular region; and (3) the total number of specimens of a species recorded in all differing districts examined in each region can be treated as the "abundance" of the species in a particular region.

The character of variability of this "abundance" between tundra subzones was estimated by the index of "relative association." The maximum values of indices F_{ij}, corresponding to the largest fraction of a species in the populations of the regions compared, were interpreted as a latitudinal "optimum" of the range, and all other values differing from –1, only as the evidence of the presence of a species in a particular region (width of the range).

It is necessary to note that, in spite of the use of objective criteria in distinguishing zonal-landscape groups, the assumed classification of springtail species of the fauna of Taimyr in relation to their association with particular zones is still rather eclectic, which is accounted for by the absence of comparable data on the boreal regions of Siberia. If a species was included in one of the fractional categories of the "Arctic species" on the basis of the reliable data on its distribution in Taimyr tundras, the identification of a species as Arctic, boreal, and polyzonal was in some cases based only on an expert assessment of the species range.

The fractional subdivisions of the category "Arctic species," used in the present study, correspond to the zonal-landscape groups suggested by Yu.I. Chernov (1978), although the landscape component was disregarded when a species was included in a particular category. This is accounted for not by the position of the author, but only by the method used for distinguishing the above groups, which is based only on the abundance indices. Together with revealing the "optimum" of the range on the basis of the highest relative abundance indices, the following concept was considered the main criterion: "hemiarctic species unite the tundra zone; hypoarctic species differentiate southern tundras; and euarctic species, which are the Arctic and hyperarctic species, indicate polar deserts." (Chernov and Matveeva, 2002). The resulting subjective classification was later additionally substantiated for the distinguished Arctic species by a cluster analysis based on Pearson's correlation coefficient (Fig. 1). In two cases, the subjective and computer variants of classification did not coincide, with the subjective variant presumably being preferable, because it takes into account the differences in the distribution of *Vertagopus brevicaudus* and all other high-Arctic species, and also the originality of the Taimyr part of the range of *Folsomia microchaeta.*

RESULTS

The values of the index of "association," which characterize the latitudinal distribution of a particular species in Taimyr, and also the zonal-landscape groups distinguished on their base, are listed in the Table.

Arctic and Non-Arctic Species of the Fauna of Taimyr

Among about 170 springtail species recorded from forestless landscapes of Taimyr, 79 species (about 47%) can be attributed to Arctic species. About ten species more, possibly also belong to this category, but it is difficult to confirm their status because they are found only locally in Taimyr. The remaining half of the regional fauna is represented by species that are, or, at least, are believed to be, boreal and polyzonal. Most of these species are abundant only in the southern half of the tundra zone; in more northern regions, including polar deserts, only separate representatives of this group are found, and polyzonal species are recorded more frequently than boreal ones (Fig. 2).

For some species, which are not included in the group of Arctic species, the largest values of F_{ij} were observed in typical or even Arctic tundras of Taimyr, rather than in southern tundras. In some cases, the artifact nature of this phenomenon, related to taxonomic problems, is evident. For example, the conspecificity of the hygrophilous (Taimyr) form of *Brachystomella parvula* and southern Siberian, evidently

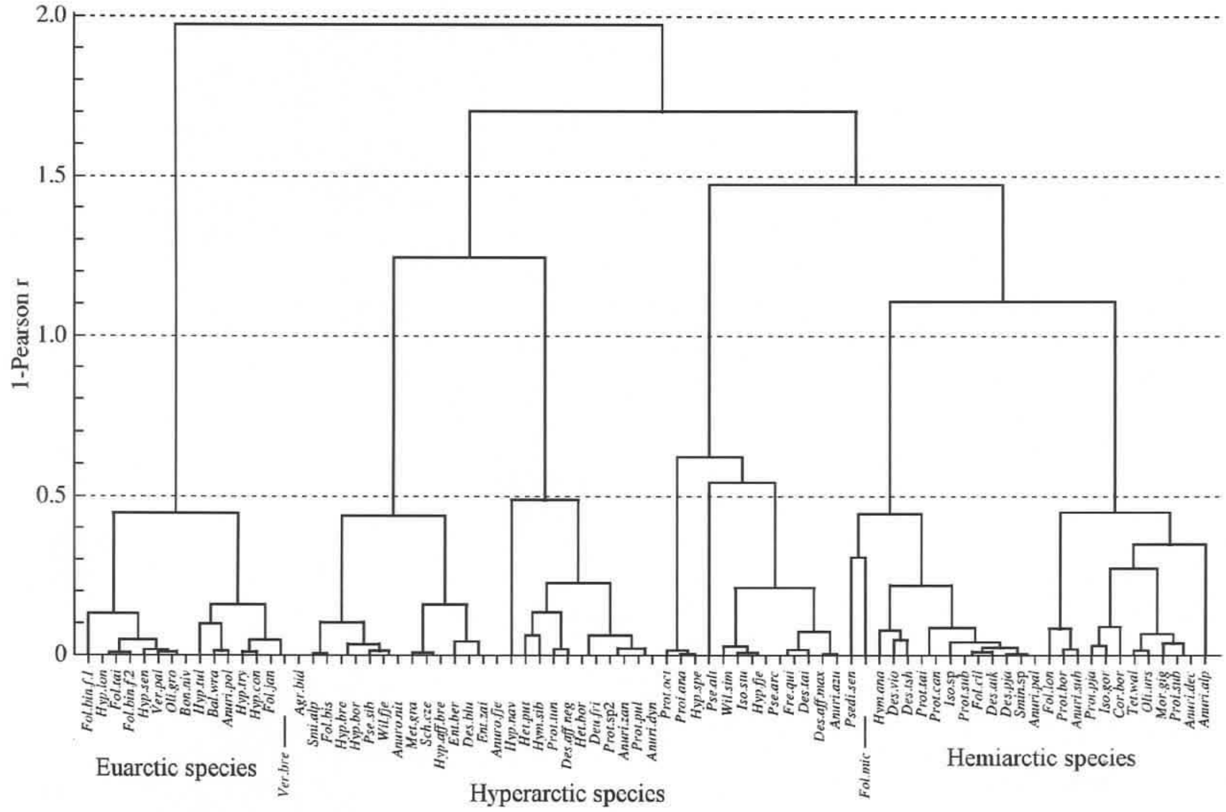

Fig. 1. Classification of Arctic species of springtails of Taimyr by the character of their latitudinal distribution, produced on the basis of a correlation between F_{ij} (method of cluster analysis, complete linkage. At $p < 0.05$, only three largest clusters are reliable).

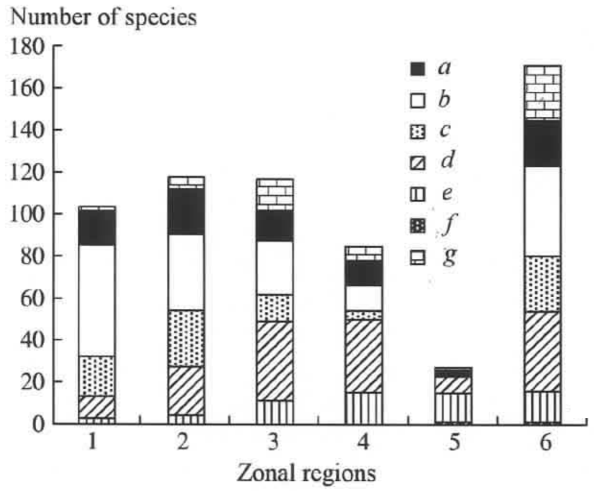

Fig. 2. Relative numbers of zonal groups in springtail faunas of various zonal regions of northern Siberia. (1) northern taiga; (2) southern tundra; (3) typical tundra; (4) Arctic tundra; (5) polar desert; (6) for all forestless landscapes of Taimyr, summarized. (*a*) polyzonal species; (*b*) boreal; (*c*) hypoarctic; (*d*) hemiarctic; (*e*) euarctic; (*f*) hyperarctic; (*g*) others.

xeroresitant populations of this "species" (Stebaeva, 1963, 1968) is doubtful. Apparently, the probability of mistakes is also high for *Folsomia monotachei* and *Willemia scandinavica* (more likely, both species are complexes of closely related forms), and *Desoria propinqua*, as well as for *Megalothorax minimus*, whose nearly cosmopolite range seems doubtful. The high value of the association index, obtained for *Folsomia diplophthalma* in typical tundras, is evidently a regional anomaly: this species was abundant and polytopic only in a single of the regions examined, this northern boreal form being retained only in meadow assemblages and in other regions. This phenomenon is evidently reliable for *Desoria neglecta*, *Sminthurides parvulus*, and *Folsomia borealis*, and two first species can be similarly attributed as Arctic species penetrating into the boreal belt via intrazonal biotopes. It is interesting that not only an increased abundance, but also a high level of polytopy is characteristic of *D. neglecta* and *S. parvulus* in the Arctic tundras. Being hygrophilous in the southern part of the tundra zone (and in more southern regions, in the forest belt), they can be attributed with good reason as "tundra

Classification of springtails of Taimyr by the character of their latitudinal distribution (based on Pesenko's "relative association" index)

Species	Northern taiga	Southern tundra	Typical tundra	Arctic tundra	Polar desert
Hyperarctic species					
Vertagopus brevicaudus	–1.000	–1.000	–1.000	–1.000	**1.000**
Euarctic species					
Agrenia bidenticulata	–0.994	–1.000	–0.999	–0.994	**0.998**
Anurida polaris	–1.000	–1.000	–0.373	–0.358	**0.702**
Ballistura wrangeliensis	–1.000	–1.000	–0.618	–0.428	**0.790**
Bonetogastrura nivalis	–1.000	–1.000	–1.000	–0.011	**0.694**
Folsomia binoculata f.2[1]*	–1.000	–1.000	–1.000	**0.474**	0.318
F. binoculata f.1	–1.000	–1.000	–0.695	–0.094	**0.676**
F. janstachi	–1.000	–1.000	–1.000	–0.934	**0.988**
F. microchaeta	–1.000	–1.000	–1.000	**1.000**	–1.000
F. taimyrica	–1.000	–0.899	–0.787	–0.111	**0.691**
Hypogastrura concolor	–1.000	–0.967	–0.814	–0.402	**0.818**
H. longispina	–1.000	–1.000	–0.862	–0.182	**0.749**
H. sensilis	–1.000	–1.000	–1.000	–0.236	**0.540**
H. trybomi	–0.974	–1.000	–0.981	–0.558	**0.896**
H. tullbergi	–0.438	–0.998	–0.546	–0.100	**0.595**
Oligaphorura groenlandica	–1.000	–0.897	–0.849	0.035	**0.629**
Vertagopus pallidus	–1.000	–1.000	–0.741	0.074	**0.596**
Number of species in the group	3	4	11	16	15
Hemiarctic species					
Anurida alpina	0.043	0.184	**0.433**	0.151	–0.652
A. azurea	–1.000	–0.940	**0.829**	0.219	–1.000
A. decemoculata	–1.000	0.518	**0.563**	0.105	–1.000
A. palustris	–1.000	–1.000	0.394	**0.762**	–1.000
A. subarctica	–0.622	**0.809**	–0.173	0.159	–1.000
Coronothryx borealis	–1.000	–0.017	**0.628**	0.126	–0.637
Desoria atkasukiensis	–1.000	–0.810	**0.652**	0.544	–1.000
D. sp. aff. *maxillosa*	–1.000	–1.000	**0.865**	0.105	–1.000
D. pjasini	–1.000	–0.976	0.473	**0.716**	–1.000
D. taimyrica	–1.000	–0.746	**0.937**	–0.374	–1.000
D. tshernovi	–1.000	–0.280	0.057	**0.808**	–0.968
D. violacea	–0.924	–0.524	0.392	**0.718**	–1.000
Folsomia ciliata	–1.000	–1.000	0.584	**0.635**	–1.000
F. longidens	–1.000	**0.591**	0.179	0.428	–1.000
Friesea quinquespinosa	–1.000	–1.000	**0.934**	–0.276	–1.000
Hymenaphorura anatolii	–0.395	–0.142	0.296	**0.677**	–1.000
Hypogastrura fjellbergi	–1.000	–1.000	**0.973**	–0.620	–1.000
H. spei	0.360	–0.965	**0.926**	–0.962	–1.000
Isotoma gorodkovi	–0.985	–0.135	0.454	**0.618**	–1.000
Isotoma sp.	–0.587	–1.000	0.576	**0.575**	–0.885
Isotomurus stuxbergi	–1.000	–1.000	**0.973**	–0.616	–1.000
Morulina gigantea	–1.000	**0.737**	0.410	–0.135	–1.000
Oligaphorura ursi	–1.000	0.446	**0.752**	–0.324	–1.000
Proisotoma ananevae	0.515	–1.000	**0.899**	–0.021	–1.000

Table (Contd.)

Species	Northern taiga	Southern tundra	Typical tundra	Arctic tundra	Polar desert
P. subarctica	–1.000	0.481	**0.554**	0.175	–1.000
Protaphorura borealis	–1.000	**0.870**	–0.247	–0.009	–1.000
Protaphorura cf. *cancellata*	–1.000	–1.000	0.055	**0.865**	–0.952
Protaphorura cf. *octopunctata*	0.386	–0.711	**0.912**	–1.000	–1.000
P. pjasinae	–1.000	0.223	0.439	**0.505**	–0.981
P. subarctica	–1.000	–1.000	**0.687**	0.520	–1.000
P. taimyrica	–1.000	–1.000	0.114	**0.863**	–1.000
Pseudanurophorus alticolus	–1.000	–0.594	**0.678**	–1.000	0.056
P. cf. *arcticus*	–1.000	–1.000	**0.934**	–0.276	–1.000
Pseudisotoma sensibilis	0.125	–1.000	0.122	**0.785**	–1.000
Sminthurus sp.	–1.000	–1.000	0.394	**0.762**	–1.000
Tetracanthella walhgreni	–1.000	0.288	**0.769**	–0.141	–1.000
Willemia similis	–1.000	–0.780	**0.905**	–0.763	–0.630
Number of species in the group	10	23	38	36	8
Hypoarctic species					
Anurida dynkengda	0.498	**0.935**	–1.000	–1.000	–1.000
A. zanokhae	0.746	**0.856**	–1.000	–1.000	–1.000
Anurophorus fjellbergi	–1.000	**1.000**	–1.000	–1.000	–1.000
Anurophorus nitrophilus	–1.000	**0.908**	0.211	–1.000	–1.000
Desoria blufusata	–0.927	**0.999**	–1.000	–1.000	–1.000
D. sp. aff. *neglecta*	0.545	**0.810**	–0.297	–0.393	–1.000
Deutonura frigida	**0.929**	0.510	–0.903	–1.000	–1.000
Entomobrya bermani	–1.000	**0.976**	–0.445	–1.000	–1.000
E. zaitzevi	–1.000	**1.000**	–1.000	–1.000	–1.000
Folsomia bisetosa	–0.655	**0.756**	0.612	–0.997	–1.000
Heterosminthurus borealis	**0.924**	0.552	–1.000	–1.000	–1.000
H. putoranae	0.672	**0.677**	0.296	*	*
Hymenaphorura sibirica	0.291	**0.908**	–0.207	–1.000	–1.000
Hypogastrura borealis	–1.000	**0.845**	0.457	–1.000	–1.000
H. sp. aff. *brevisensillata*[2]	–0.306	**0.988**	–1.000	–1.000	–1.000
H. cf. *brevis*	–1.000	**0.865**	0.394	–1.000	–1.000
H. navicularis	**0.994**	–0.569	–1.000	–1.000	–1.000
Metisotoma grandiceps	–0.222	**0.986**	–1.000	–1.000	–1.000
Protaphorura cf. *pulvinata*	0.452	**0.942**	–1.000	–1.000	–1.000
P. tundricola	0.491	**0.807**	–0.094	–0.483	–1.000
Protaphorura sp. 2[3]	**0.823**	0.791	–1.000	–1.000	–1.000
Pseudachorutes sibiricus	–1.000	**0.944**	–0.041	–1.000	–1.000
Schaefferia czernovi	–0.366	**0.990**	–1.000	–1.000	–1.000
Sminthurinus alpinus	–0.449	**0.721**	0.635	–0.947	–1.000
Willemia fjellbergi	–1.000	**0.921**	0.136	–1.000	–1.000
Number of species in the group	17	25	13	4	0
Boreal species					
Arrhopalites principalis	**0.965**	0.217	–1.000	–1.000	–1.000
Agrenia riparia	**0.962**	0.268	–1.000	–1.000	–1.000
Anurida confines	**0.992**	–0.500	–1.000	–1.000	–1.000

Table (Contd.)

Species	Northern taiga	Southern tundra	Typical tundra	Arctic tundra	Polar desert
A. nadezhdae	**1.000**	–1.000	–1.000	–1.000	–1.000
Anurophorus palaearcticus	**0.984**	–0.181	–1.000	–1.000	–1.000
Ballistura cf. *borealis*	–1.000	**0.981**	–0.530	–1.000	–1.000
Desoria alaskensis	**0.506**	0.153	0.189	0.425	–1.000
D. neglecta	–0.961	0.473	0.022	**0.609**	–1.000
D. propinqua	–0.964	–0.568	0.460	**0.686**	–1.000
D. ruseki	**0.876**	0.701	–0.951	–1.000	–1.000
D. violacea auct.	**0.843**	0.765	–1.000	–1.000	–1.000
Dicyrtoma cf. *christinae*	**1.000**	–1.000	–1.000	–1.000	–1.000
D. ghilarovi	**1.000**	–1.000	–1.000	–1.000	–1.000
Drepanura quadrilineata	**1.000**	–1.000	–1.000	–1.000	–1.000
Endonura reticulata	**0.962**	0.217	–1.000	–1.000	–1.000
Entomobrya cf. *marginata*	**1.000**	–1.000	–1.000	–1.000	–1.000
E. nivalis	**1.000**	–1.000	–1.000	–1.000	–1.000
E. obensis	**1.000**	–1.000	–1.000	–1.000	–1.000
Entomobrya sp.	**1.000**	–1.000	–1.000	–1.000	–1.000
Folsomia borealis	–1.000	0.962	0.346	**0.774**	–1.000
F. diplophthalma	–0.091	0.076	**0.903**	–0.873	–1.000
F. palaearctica	–0.232	**0.691**	–0.214	–0.214	–1.000
Friesea claviseta	**0.999**	–1.000	–0.945	–1.000	–1.000
F. mirabilis	**0.994**	–1.000	–0.709	–1.000	–1.000
F. truncata	**0.800**	0.806	–0.883	–1.000	–1.000
Grananurida baicalica	**1.000**	–1.000	–1.000	–1.000	–1.000
Heterosminthurus bilineatus	**0.854**	0.748	–1.000	–1.000	–1.000
H. chaetocephalus	–1.000	**1.000**	–1.000	–1.000	–1.000
H. stebaevae	**1.000**	–1.000	–1.000	–1.000	–1.000
H. umbonicus	**1.000**	–1.000	–1.000	–1.000	–1.000
Hypogastrura brevisensillata[2]	–1.000	–1.000	**1.000**	–1.000	–1.000
H. lapponica	**0.860**	0.750	–1.000	–1.000	–1.000
H. sigillata	**1.000**	–0.988	–1.000	–1.000	–1.000
Isotoma riparia	**0.924**	0.552	–1.000	–1.000	–1.000
Isotomiella minor	**1.000**	–1.000	–1.000	–1.000	–1.000
Isotomurus plumosus	–1.000	0.999	–0.963	–1.000	–1.000
Lepidocyrtus violaceus	**0.634**	0.606	0.461	–0.809	–1.000
Micranurida pygmaea	0.777	0.827	–0.904	–1.000	–1.000
M. spirillifera	**1.000**	–1.000	–1.000	–1.000	–1.000
Micraphorura absoloni	**1.000**	–1.000	–1.000	–1.000	–1.000
Morulina theeli	**1.000**	–1.000	–1.000	–1.000	–1.000
Neanura sp. aff. *muscorum*	**0.966**	0.213	–1.000	–1.000	–1.000
Pachyotoma sp.	**1.000**	–1.000	–1.000	–1.000	–1.000
P. crassicauda	**0.854**	–1.000	0.643	–1.000	–1.000
Parisotoma ekmani	0.315	**0.938**	–0.963	–0.690	–1.000
P. reducta	–1.000	0.235	**0.527**	0.442	–1.000
Proisotoma sp.	**0.984**	–1.000	–1.000	–0.459	–1.000
Protaphorura bicampata	–0.905	**0.916**	–0.203	–0.405	–1.000
P. jacutica	0.729	**0.865**	–1.000	–1.000	–1.000

Table (Contd.)

Species	Northern taiga	Southern tundra	Typical tundra	Arctic tundra	Polar desert
P. flavorufulus	**0.948**	0.405	−1.000	−1.000	−1.000
P. subuliginata	**1.000**	−1.000	−1.000	−1.000	−1.000
Pseudanurophorus binoculatus	**0.974**	0.068	−1.000	−1.000	−1.000
Ptenothrix cf. *setosa*	**1.000**	−1.000	−1.000	−1.000	−1.000
Secotomodes sibiricus	**0.961**	0.275	−1.000	−1.000	−1.000
Sphaeridia leutrensis	**0.516**	0.481	0.214	0.131	−1.000
Supraphorura furcifera	**0.815**	0.260	−0.313	0.144	−1.000
Tantulonychiurus volinensis	−1.000	**0.758**	0.629	−1.000	−1.000
Tomocerus minutus	**0.949**	0.379	−0.943	−1.000	−1.000
T. sibiricus	**1.000**	−1.000	−1.000	−1.000	−1.000
Vertagopus pseudocinereus	**0.949**	−1.000	−0.610	−0.038	−1.000
Willemia anophthalma	**0.970**	0.119	−0.939	−1.000	−1.000
W. denisi	**0.834**	0.773	−0.948	−1.000	−1.000
W. trisphaerae	−1.000	**1.000**	−1.000	−1.000	−1.000
Xenylla betulae	**0.994**	−0.592	−1.000	−1.000	−1.000
Xenyllodes armatus	**0.781**	−0.983	0.756	−1.000	−1.000
Number of species in the group	57	40	27	13	0
Polyzonal species					
Brachystomella parvula	−0.204	−0.026	0.250	**0.655**	−1.000
Deuterosminthurus pallipes principalis	**1.000**	−1.000	−1.000	−1.000	−1.000
D. pallipes repanda	**0.854**	0.748	−1.000	−1.000	−1.000
Folsomia manolachei	−0.173	0.148	0.185	0.632	−1.000
F. quadrioculata	0.346	**0.572**	−0.122	0.396	−1.000
F. rossica	0.396	**0.949**	−1.000	−1.000	−1.000
Folsomides parvulus	**1.000**	−1.000	−1.000	−1.000	−1.000
Isotoma cf. *viridis*	0.081	**0.827**	0.249	−0.695	−1.000
Megalothorax minimus	0.138	0.259	−0.012	**0.382**	−0.570
Mesaphorura tenuisensillata	**0.998**	−0.860	−1.000	−1.000	−1.000
Parisotoma notabilis	0.783	**0.811**	−0.972	−0.826	−1.000
Podura aquatica	**0.752**	0.588	−0.132	−0.237	*
Proisotoma ladaki	−1.000	**1.000**	−1.000	−1.000	−1.000
Sminthurides aquaticus	**0.854**	0.748	−1.000	−1.000	−1.000
S. malmgreni	**0.748**	−0.114	−0.465	0.534	−1.000
S. inaeuqalis armatus	−1.000	0.748	−0.041	−1.000	−0.156
S. parvulus	0.163	0.258	0.317	**0.440**	−1.000
S. schoetti	**0.744**	0.532	0.104	−0.332	−1.000
S. signatus	−1.000	**0.953**	−0.132	−1.000	−1.000
Stenacidia violacea	−1.000	**0.865**	0.394	−1.000	−1.000
Wankeliella intermedia	−1.000	**1.000**	−1.000	−1.000	−1.000
Willemia scandinavica	−1.000	0.231	−0.344	**0.725**	−0.754
Xenylla martynovae	**0.962**	−1.000	0.070	−1.000	−1.000
Number of species in the group	17	20	15	11	3
Species locally found in Taimyr					
Anurida beringi	−1.000	−1.000	1.000	−1.000	−1.000
A. papillosa	−1.000	−1.000	1.000	−1.000	−1.000

Table (Contd.)

Species	Northern taiga	Southern tundra	Typical tundra	Arctic tundra	Polar desert
Archisotoma besselsi	–1.000	–1.000	0.643	0.575	–1.000
A. polaris	–1.000	–1.000	–1.000	1.000	–1.000
Folsomia altamontana	–1.000	–1.000	–1.000	–1.000	1.000
F. amplissima					*
F. cryptophila	–1.000	–1.000	1.000	–1.000	–1.000
F. cf. *ozeana*	–1.000	–1.000	1.000	–1.000	–1.000
F. sexoculata	–1.000	–1.000	–1.000	1.000	–1.000
F. sp. gr. *dorvensis*			*		
Heterosminthurus linnaniemi	–1.000	1.000	–1.000	–1.000	–1.000
Hypogastrura sp. gr. *armata*	–1.000	1.000	–1.000	–1.000	–1.000
H. palustris	–1.000	–1.000	1.000	–1.000	–1.000
H. rangkuli	–1.000	–1.000	–0.132	0.914	–1.000
Isotomodella sp.			*		
Isotomurus sp. gr. *palustris*	–1.000	1.000	–1.000	–1.000	–1.000
Micraphorura sp.	–1.000	1.000	–1.000	–1.000	–1.000
Multivesicula dolomitica			*		
Oligaphorura sp. aff. *ursi*	–1.000	–1.000	1.000	–1.000	–1.000
Parisotoma longa	–1.000	–1.000	1.000	–1.000	–1.000
Protaphorura s. l[4]	–1.000	1.000	–1.000	–1.000	–1.000
Rusekianna sp.	1.000	–1.000	–1.000	–1.000	–1.000
Sminthurus denticulatus	1.000	–1.000	–1.000	–1.000	–1.000
Sminthurus (?) cf. *silvestris*	–1.000	1.000	–1.000	–1.000	–1.000
Sphaeridia pumilis			*	*	
Thalassaphorura duplopunctata	–1.000	–1.000	–1.000	1.000	–1.000
Uralaphorura cf. *shilovi*	–1.000	–1.000	1.000	–1.000	–1.000
Willemia multilobata	–1.000	–1.000	–1.000	1.000	–1.000
Xenylla humicola	–1.000	–1.000	1.000	–1.000	–1.000

Bold face marks values of the "association" index highest for a species; latitudinal regions in which a species was recorded are placed in shaded cells. Asterisk (*) marks solitary findings.

[1] Two forms well differing in the appearance are found in the north of Taimyr; however, their morphological differences are insufficient for these species to be clearly distinguishable (Potapov and Babenko, 2000).

[2] Two different species are named *H. brevisensillata* in the fauna of the eastern Palaearctic; one of these is widespread in the entire Siberia (and in North America), and the other is, probably, associated with northern forests. It is unclear, which of these species was mentioned by R. Yosii (Babenko *et al.*, 1994).

[3] A species with a 32/022/33332 and without pseudo-ocelli on subcoxae.

[4] A species with a 33 (2)/02(3)3/33342 pseudocellular formula, Abd. 1–3 c s'.

species" in the Arctic subzone because of the clearly pronounced preference of zonal communities. The situation with *F. borealis* is more complicated, because this species is equally characteristic of mesophytious spruce forests of the forest belt (Kuznetsova, 2003) and zonal communities of tundras, and only in the northernmost extremity of its range (in the Arctic subzone) moves to the warmer part of the landscape profile.

Hyperarctic Species

A single species, *Vertagopus brevicaudus*, was included in this category. This species is not only more abundant in polar deserts, but is limited in its range just to these marginal landscapes (Franz Joseph Land, Severnaya Zemlya, Cape Chelyuskin in Taimyr, and the northwestern part of the Canadian Arctic Archipelago). The fact of such a strict association is rather reliable, but the factors determining the southern border of the range are unclear. Some problems related to the settling process could be assumed for island populations, but this is apparently inapplicable to the mainland part of the range of this species. Being one of the most noticeable dwellers of very different communities, including zonal ones, on Cape Chelyuskin (Serebryanka River, 77°36′N, 103°49′E), *V. brevicaudus* was not found in the northernmost extremity of Arctic tundras eastwards (Pronchishchev Coast, Rybnaya River, 76°38′N, 111°00′E) or westwards (Khariton Laptev Coast, Middendorf Bay, Opalovaya River, 75°56′N, 94°13′E). The climatogenic origin of such a distinct southern border is also very doubtful, because differences between so closely lying northern regions can hardly be significant.

Euarctic Species

The most characteristic Arctic species of springtails, whose fraction increases at higher latitudes, were included in the group of euarctic species. For most of these species, the highest values of F_{ij} were recorded not even in arctic tundras, but in polar deserts; i.e., they could also be treated as hyperarctic species. The rather wide distribution of the majority of euarctic species in the tundra zone hampers such a treatment. The larger fraction of species of this group in the population of Arctic deserts (in comparison with the Arctic tundras) may be due to a strong impoverishment of polar-desert faunas on the background of the very abundant population. The majority of springtail species included in the group of euarctic species (excluding *Hypogastrura concolor*, *Folsomia microchaeta*, and *Vertagopus pallidus*), are typical hygrophilous species in the tundra zone, and are usually polytopic species in more northern regions of polar deserts. Frequently, the ranges of euarctic species are not limited to the Arctic regions, and they are found in more southern regions, and not only in highlands, but also in the forest belt, usually, in specific habitats (Babenko, 2002). *F. microchaeta*, a species which is characteristic only of a narrow strip of Arctic tundras of Taimyr, occupies a somewhat isolated position. Apparently, this originally mountain species finds the best environmental conditions just in the zonal assemblages of the Arctic subzone, rich in exposed areas. It is noteworthy that in more southern regions of Taimyr, this species has been recorded only from mountain tundras in the Dakstas Ridge (Ananyeva, 1973).

Hemiarctic Species

The largest fraction of the Arctic species was included in the group of hemiarctic species. This group is rather heterogeneous: it combines species with the highest F_{ij} value in the typical, Arctic, and, less frequently, southern tundras. However, representatives of just this group are "the most active in the zonal assemblages of the largest territories of the tundra zone" (Chernov and Matveeva, 2002, p. 44) and determine the common character of the springtail fauna within this typological group. A rather abundant group of hemiarctic species also penetrates into polar deserts, thereby significantly raising the diversity of the springtail fauna of this region. However, being found as solitary specimens in local biotopes, representatives of this group are unimportant in the cenotic respect. Apparently, hemiarctic springtail species may be widespread in more southern non-tundra regions; however, their distribution in the boreal belt must be sporadic. As can be seen in Fig. 3, the range of *Morulina gigantea*, a member of the group of hemiarctic species, can be named trans-Siberian. However, in southern areas of the range, S.K. Stebaeva found less than 10 specimens of this, rather noticeable (up to 3–4 mm long) springtails species in the course of her long-term studies.[1] At the same time, springtails trapped during a day will include no less than 10 specimens of the hemiarctic group in each trap nearly in every community of southern tundras. The group of hemiarctic species is no less heterogeneous in their biotopic preferences as in the character of their distribution in the tundra zone of Taimyr. It includes stenotopic and polytopic forms, both from zonal communities and from various intrazonal stations.

Hypoarctic Species

The group of hypoarctic species, i.e., species with the optimum of their abundance at the southern border of the tundra zone, is rather clearly distinguished. At the same time, the subdivision of species into boreal and hypoarctic ones solely on the basis of F_{ij} index meets difficulties, because the data available cover

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[1] According to new unpublished data, this species is abundant in mountain regions of Yakutia (Suntar-Khayata Mountain Range). However, this finding does not change the status of this species as a member of the hemiarctic group.

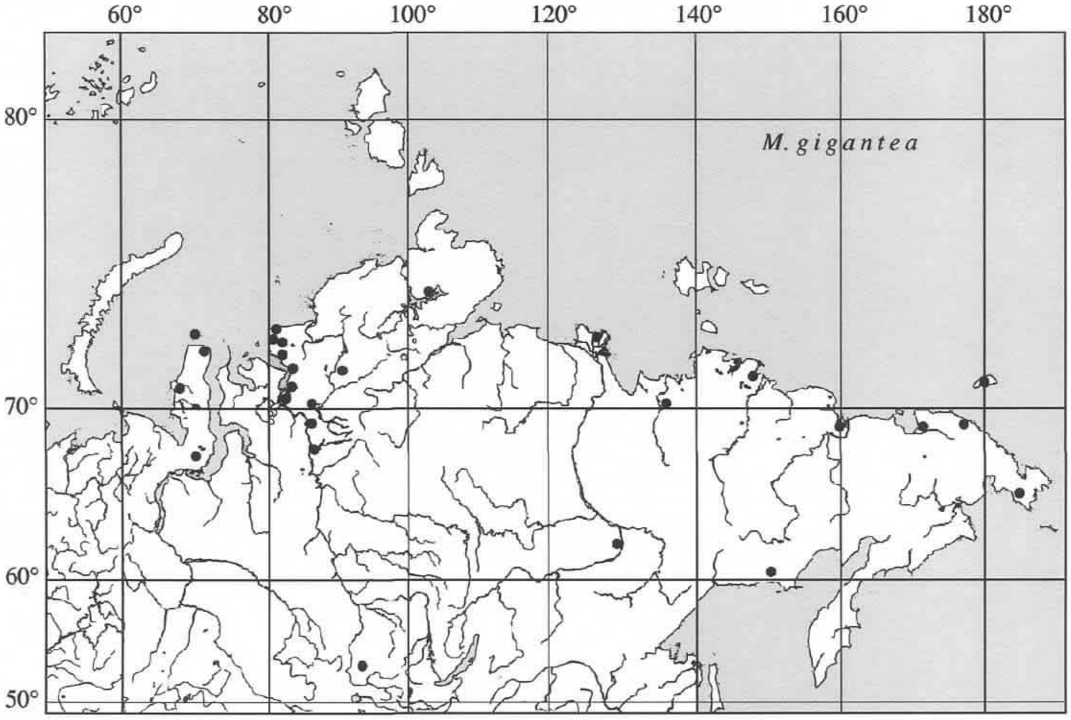

Fig. 3. Occurrence of a typical hemiarctic species, *Morulina gigantea* (from Babenko and Fjellberg, 2001).

only the northernmost part of the taiga zone, where boreal and hypoarctic species could be found in equally large numbers. Therefore, in arguable cases, the biotopic distribution of species in southern tundra landscapes was also taken into account. For example, in spite of the higher values of F_{ij} in the taiga region, such species as *Deutonura frigida*, *Heterosminthurus borealis*, and *Protaphorura* sp. 2, successfully dwelling in non-shrub zonal communities of southern tundras, were included in the group of hypoarctic species. One more "problematic" species, *Hypogastrura navicularis*) was included in the group of hypoarctic species, because its range occupies a narrow border strip between the tundra zone and the forest belt from northeastern parts of European Russia to middle Siberia.

Penetrating into typical tundras, the majority of hypoarctic species are found there occasionally or very rarely, as solitary specimens, excluding 4 species: *Desoria* sp. aff. *neglecta*, *Folsomia bisetosa*, *Protaphorura tundricola*, and *Sminthurinus alpinus*. These species have been recorded even from the northern subzone; they occupy an intermediate position between hypoarctic and hemiarctic species. Their hypoarctic status is determined by the relative polytopy in southern tundras and the abrupt change of the preferenda even in typical tundras, where all these 4 species are dwellers of slope meadows with rather warm conditions.

Arctic-Alpine Species

The most clearly disjunctive Arctic-Alpine range is characteristic of *Folsomia altamontana*. This species has been described from high mountains of Himalayas; it is abundant in the Alpine plateau of the Putorana, and several specimens have been recorded from Novaya Zemlya and Novosibirsk Islands. In the springtail fauna of Taimyr, several more species are also of the Alpine origin, which is confirmed by their recent distribution. For example, the ranges of *Agrenia bidenticulata* [euarctic species in Taimyr, but a common species in the mountains of middle Europe (Fjellberg, 1986)], *Corynothrix borealis* [a hemiarctic species, recorded from Tien Shan (Martynova, 1970) and Rocky Mountains in Colorado (Fjellberg, 1984)] and the closely related species *F. microchaeta* (recorded from Arctic regions of the Palaearctic Region and also in the mountains of Scandinavia and Yakutia (Potapov, 2001) and northern Canada (Hammer, 1953)], are similar. However, distinguishing these species as a separate category is unjustified, because it reflects only the faunal–historical relations, whereas the recent latitudinal distribution of the forms mentioned is different. Nevertheless, it is very difficult to find a place for *F. altamontana* within the zonal-landscape groups suggested, because this species is too small in number in polar deserts to be included in the group of hyperarctic species, and has never been found in the tundra. Hence, it cannot be a euarctic, hemiarctic, or hypoarctic species.

Species with Unclear Status

A rather large number of species inhabiting Taimyr was excluded from our analysis. Interpretation of the latitudinal distribution of these species in Taimyr is difficult for various reasons. This group includes species that are simply very rare in Taimyr and are known only from several specimens, rather abundant species recorded only in one of the regions examined, several incompletely determined species, and also typical littoral forms whose presence in a particular tundra region depends only on its closeness to the seacoast. Specific tundra dwellers can probably be found among these species. For example, *Sminthurus* (?) cf. *silvestris* and *Hypogastrura* sp. gr. *armata* are very characteristic (being abundant and polytopic species) of the southern tundras of Taimyr. Only their unclear taxonomic status (i.e., unknown character of distribution) makes impossible combining these species with the typical hypoarctic species. In the optimal part of their ranges, two species of the genus *Anurida* (*A. beringi* and *A. papillosa*) can also be treated as hypoarctic species; however, only solitary specimens of these species have been recorded from Taimyr (in the western and eastern extremities of the range, respectively).

DISCUSSION

The fraction of Arctic species in the fauna of Taimyr, in comparison with analogous indices known for other animal and plant groups, is not only surprisingly high, but does not coincide with the tendencies observed (Chernov and Matveeva, 2002). It is assumed that the number of typical Arctic forms in a taxon directly depends on its phylogenetic level. For example, it is the highest in flowering plants and negligible in lichens and mosses. The most primitive archaic groups not only demonstrate, because of their originally strong adaptive abilities in relation to the Arctic environment (Chernov, 1984, 1988), the highest number of representatives in the tundra zone (Chernov, 2002), but, as a rule, have wide species ranges that are nearly independent of recent zonal borders. The population of the Arctic environment by progressive, highly organized forms, by contrast, needs significant adaptive reconstructions, which predetermines the formation of specific Arctic species (Chernov and Matveeva, 2002). Springtails, undoubtedly, belong to the first group of rather primitive taxa, primordially adapted to the environmerntal conditions of the Arctic Region. Therefore, the high "Arctic specialization" of the springtail fauna, revealed in the present study, clearly needs explanation.

It is possible to assume that this phenomenon is mainly the result of the ambiguity in the designation of the term "Arctic species," and such a high degree of preference to Arctic biotopes by springtails is determined by the method applied, when only the quantitative character of their distribution in the subarctic landscapes, rather than their ranges, was taken into account. For certain, a part of species distinguished as Arctic species, dwell outside the limits of higher-latitude landscapes and penetrate far southwards via highlands and different intrazonal elements of landscapes,[2] i.e., from the chorological point of view, the overwhelming majority of these species, excluding *V. brevicaudus* and, probably, part of euarctic species, are meta-Arctic, Arctic-mountain, or Arctic-boreal , rather than strictly Arctic species. Nevertheless, the categories "Arctic," "boreal," etc., are rather ecological than spatial. Therefore, it is more logical to take into account the character of distribution, rather than the borders of the range, when attributing a species as a member of a particular category.

Probably, a high degree of Arctic species among springtails can be partly accounted for by the region of investigation. The Taimyr Peninsula is one of the most severe Arctic regions. There, the southern borders of the tundra zone run at significantly higher latitudes than in any other area of Euro-Asiatic Subarctic Region. Therefore, the fraction of Arctic species in the biota of this region is naturally larger. For example, the fraction of Arctic species (even in the widest interpretation of this category, including meta-Arctic and Arctic-Alpine species) in the flora of vascular plants of the Russian Arctic Region does not exceed 40% of the whole flora (Chernov and Matveeva, 2002), only higher Arctic elements (without hypoarctic ones) constitute more than 60% of the entire list of higher plants in Taimyr (Matveeva, 1998). Probably, a similar pattern is characteristic of animals. It is necessary to note that the classification assumed is treated by the author as a strictly regional classification. Significant changes in the zonal distribution of species and their purely ecological characteristics are not only possible, but are highly probable (Chernov, 1999).

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[2] Probably, some of the so-called Arctic species can also be common in plain regions of central Siberia, which are unexamined in this respect.

In spite of the vast species ranges of springtails, the character of the latitudinal distribution of species of this group in Taimyr differs only slightly from that typical of other animal taxa (Chernov, 1975). Virtually all features of the zonal-landscape distribution of species, described in the literature, can be exemplified by springtails, although the development of these characters is usually noticeable only on the quantitative level.

Firstly, it is necessary to note that, similarly to the majority of taxa characteristic of the Subarctic Region, changes in the fauna of this group from the south to the north cannot be understood as a unidirectional process of impoverishment, "cleaning" of faunas to remove alien "southern" elements. The opposite tendency, i.e., enrichment of local faunas with species best of all adapted to higher Arctic latitudes, is quite noticeable. The latter process is significantly weaker, but its occurrence is very symptomatic. The approximately same species richness of local faunas of southern and typical tundras in Taimyr is, apparently, accounted for by the equilibrium in development of these processes. To the north, the process of impoverishment clearly prevails in comparison with the appearance of "new" forms, which results in a strong decrease in the species richness in tundras and polar deserts.

Species with the better capabilities to use various intrazonal habitats possess the highest expansion and adaptive potential in the tundra zone. By contrast, association with placor communities is a character meaning the narrow specialization, which limits the possibility of spreading into various zones (Chernov, 1975, 1978). This concept is well applicable to springtails. It is the hygrophilous species of this group, and also quite a number of dwellers of intensively warmed stations, that are the most widespread in the tundra zone and beyond its limits. The number of Arctic species among dwellers of zonal-tundra communities is noticeably larger (Babenko, 2003).

Advanced settling possibilities are also characteristic of species predisposed to synanthropy. Polyzonal plastic forms prevail among synanthropous species of other taxa in the tundra zone, and no single autochthonous Arctic species, an increase in whose range would be directly associated with this tendency, has been known so far (Chernov, 1978). The synanthropy is not very much characteristic of springtails as a taxonomic group. However a single rather brilliant example exists: such a thermophilous species as *Willowsia buski* has been recorded from Taimyr. It is interesting that this finding is far from being the first one. This species has been listed (under the name *Sira flava* Agren, 1904) in the fauna of Spitsbergen since 1930 (Thor, 1930) and is regarded as an accidentally brought ecdemic species (Fjellberg, 1994). The mass breeding of this species was observed in living rooms of a hotel in Dixon Island in 1983. The number of specimens was so large that they covered a windowsill as an all-over carpet. Strange as it may seem, but this species was found not in the same year near a mainland village in a trace recording in a natural habitat (about 2 km from the nearest quarters), and this occurred in a nival community, rather than in a meadow. Unfortunately, no data are available concerning the subsequent fate of this "natural" population. In rooms of the hotel, separate specimens could be seen during several following years, but no mass breeding has been observed any more.

A distinct increase in the latitudinal extension of the range in more northern forms (Chernov, 1978б 1999) is also well seen in springtails. For example, the fraction of species with circumpolar or nearly circumpolar ranges is significantly larger among species included in the group of euarctic species, compared with hemiarctic or hypoarctic species, many of which have distinct meridian borders.

As in many other taxa, widespread plastic species with ranges virtually independent of zonal borders are present among springtails of the tundra zone. Although they rather frequently dominate in tundra assemblages, their total number is rather small (and frequently directly depends on the level of taxonomic development of a taxon). More or less narrow borders of the "optimum" of distribution within a particular tundra subzone are characteristic of the majority of species; outside this zone, species either disappear or strongly change the character of their biotopic distribution, i.e., different forms of development of the "law of the environment leveling" (Chernov, 1974, 1975). At the border of the range, a species can even be abundant in conditions strongly different from its typical habitats. For example, the mainly marsh-dwelling, in the forest belt, *Xenyllodes armatus* is found at the center of the tundra zone only locally (dryad communities on dry stony slopes), but occasionally reaches a density of several hundred specimens per square decimeter (Ananyeva, 1973), which is significantly higher than the level typical of the forest belt (see, e.g., Kuznetsova, 1988).

Naturally, the latitudinal borders of ranges are particularly relative, being not always directly determined by climatic factors. For example, although the northern border of the forest is a very distinct frontier for many species (e.g., for such a widespread and nearly polytopic, in the forest belt, species as *Isotomiella minor*), some forest forms disappear gradually, finding suitable conditions also in the south of the tundra zone. For example, the distribution of two such typical base-of-tree trunk-and-bark dwellers as *Anurophorus palaearcticus* and *Vertagopus pseudocinereus* is highly illustrative. The depth of penetration of the first species into tundras is very insignificant and is entirely determined by the northern border of distribution of some larches, with large local populations of *A. palaearcticus* occasionally found under the bark. By contrast, *V. pseudocinereus*[3] is never abundant in tundra communities, but solitary specimens of this species were recorded nearly in all regions examined, and not only in coastal regions, where the probability of its permanent bringing with wood is rather high. Apparently, this, allochthonous for the tundra, species could find a suitable niche even in such unusual conditions.

Summarizing, I would like to underline that the aforesaid does not contradict the concept "...that soil as a habitat favors a weaker dependence of a species on climatic gradients" (Chernov, 1974, p. 128). This is an undisputable fact. In this context, it is even more interesting that many common tendencies observed in the intrazonal distribution of species in the subarctic zone, characteristic of dwellers of exposed habitats, are also rather clearly manifested in such an archaic soil group as collembolans.

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[3] Although this species has been described from Spitsbergen (Fjellberg, 1975), its distinct association with under-bark stations of northern forests is beyond doubt (Potapov, 2001).

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